

LANDSCAPE CHARACTERISTICS OF NORTHERN SPOTTED OWL NEST SITES IN MANAGED FORESTS OF NORTHWESTERN CALIFORNIA

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ABSTRACT.—We investigated vegetative and topographic characteristics of forest landscapes surrounding Northern Spotted Owl (*Strix occidentalis caurina*) nest sites on managed timberlands in northwestern California. Nest sites occurred primarily in young (31–60-yr old) forests of redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*). We compared 60 Northern Spotted Owl nest landscapes (0.8-km radius circle centered on the nest site) with 60 randomly selected landscapes. Vegetative type and age class were used to classify forest stands within the landscape. Landscape features differed between nest sites and random sites (Wilks' $F = 6.073$, $P < 0.001$) suggesting that nest-site selection was correlated with landscape level features. Nest landscapes had greater amounts of forest in the 31–45 and 46–60 yr-old age classes, and a greater amount of total edge. In addition, nest sites were located lower on slopes. In our study area, dusky-footed woodrats (*Neotoma fuscipes*) were the major prey species. Edges may provide opportunities for owls to prey on woodrats that are abundant in early seral habitats. The coastal forests of the redwood zone have unique characteristics that contribute to rapid development of Northern Spotted Owl habitat. These include coppice growth (i.e., vegetative reproduction) of redwoods and several hardwood species, favorable growing conditions and the occurrence of major prey species in young seral habitats. Despite differences in habitat types and age classes, Northern Spotted Owl nest-site selection in these young, managed forests showed some consistent patterns with other portions of the owls' range.

KEY WORDS: *Northern Spotted Owl*; *Strix occidentalis caurina*; *landscape pattern*; *nest-site selection*; *managed forest*; *redwoods*; *northwestern California*.

Características paisajísticas de los sitios de anidación de *Strix occidentalis caurina* en bosques manejados del noroeste de California

RESUMEN.—Investigamos las características topográficas y de vegetación de los paisajes de bosques alrededor de los sitios de nidos de *Strix occidentalis caurina* en bosques manejados del noroeste de California. Los sitios del nido fueron encontrados principalmente en bosques jóvenes (31–60 años de edad) de *Sequoia sempervirens* y en *Pseudotsuga menziesii*. Comparamos 60 paisajes de los sitios del nido (0.8 km de radio del círculo centrado en el sitio del nido) con 60 paisajes seleccionados al azar. El tipo de vegetación y la edad por clase fueron utilizados para clasificar los árboles dentro de los paisajes. Las características paisajísticas difirieron entre los sitios del nido y los sitios seleccionados al azar (Wilks' $F = 6.073$, $P < 0.001$) lo que sugiere que la selección del sitio de anidación fue correlacionada con las características del nivel de paisaje. Los paisajes del nido tuvieron mas cantidad de bosque en los 31–45 y 46–60 años de clases de edad y mayor cantidad de borde total. Adicionalmente, los sitios del nido fueron localizados en la parte baja de la ladera. En nuestra área de estudio *Neotoma fuscipes* fue la especie de presa mayor. Los bordes proveen muchas oportunidades para la depredación de ratas las cuales son abundantes en este tipo de habitats. Los bosques costeros de maderas rojas poseen características únicas que contribuyen al rápido desarrollo de habitat para *Strix occidentalis caurina*. Esto incluye el crecimiento del sotobosque (reproducción vegetativa) de maderas rojas y especies de maderas duras, como también las condiciones favorables de crecimiento para la presencia de presas mayores en habitats jóvenes. A pesar de las diferencias en tipos de habitats y de clases por edad, la selección de sitios de nido por

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parte de los buhos en estos bosques jóvenes y manejados mostró algunos patrones de consistencia con otras porciones de su rango.

[Traducción de César Márquez]

The Northern Spotted Owl (*Strix occidentalis caurina*) is associated primarily with old forests throughout its range (Forsman et al. 1977, Gould 1977, Forsman et al. 1984, Solis and Gutiérrez 1990). Loss of habitat, due to timber harvest, has been implicated as the major threat to the subspecies' continued existence (Forsman et al. 1984, Federal Register 1990). The Northern Spotted Owl is reported to be a forest-interior species that has a large home range that includes a significant amount of older forest (Thomas et al. 1990).

Studies of the distribution of owl habitat at a landscape level consistently indicate that larger amounts of old-growth forest surround Northern Spotted Owl activity centers than at random locations (Ripple et al. 1991, Blakesley et al. 1992, Lehmkühl and Raphael 1993). In addition, their home-range size may be inversely related to the proportion of old-growth forest within the home range and the amount of old growth within home ranges is less variable than home range size itself (Carey et al. 1990).

Generally, Northern Spotted Owls are less abundant in managed young forests (Forsman et al. 1977, Forsman 1988). However, they have been frequently reported in young forests within the coastal redwood (*Sequoia sempervirens*) zone of California that has little or no old-growth habitat present (Thomas et al. 1990). Little is known about the forest characteristics surrounding owl nest sites in these managed landscapes. Therefore, our objective was to describe the vegetative and topographic characteristics of the forest landscape surrounding Northern Spotted Owl nest sites in managed forests of northwestern California. Specifically, we tested the null hypothesis that no differences in landscape-level variables existed between nest sites and random sites.

STUDY AREA

The study area was located in Humboldt and Del Norte counties in northwestern California on forestlands owned by Simpson Timber Company (STC) (Fig. 1). In this region, STC manages approximately 1200 km² of land parcels that vary in size from 16–200 km². Most of the study area was located within 32 km of the Pacific Ocean. The study area was located within the Redwood Vegetation Zone (Mayer 1988) and corresponds to the Northern California Coast Range Physiographic Province

(Thomas et al. 1990). The region has a maritime climate with mild winters and cool summers typified by valley fog and high humidity. Mean annual rainfall is 280 cm near the coast to 102 cm inland. Most precipitation occurs during winter months. Mean annual temperature is 11°C with little temperature fluctuation throughout the year (mean temperature in January = 8°C, July = 15°C) (Zinke 1988). Elevation ranges from near sea level to approximately 915 m.

The dominant vegetation types were redwood, redwood-Douglas-fir, Douglas-fir (*Pseudotsuga menziesii*) and oak (*Quercus* spp.) woodlands (Zinke 1988). Oak woodlands were predominately tanoak (*Lithocarpus densiflorus*) with California black oak (*Quercus kelloggii*) and Oregon white oak (*Quercus garryana*) on drier sites. Forest zonation was produced by changes in climate, soil type and topography (Zinke 1988). Redwoods were limited to a coastal strip about 8–56 km wide that received adequate summer fog and mild temperatures (Fowells 1965). As conditions become drier away from the coast, Douglas-fir replaced redwood as the predominant conifer and hardwoods become more abundant. On most sites, the conifer forest types were associated with hardwood species such as tanoak, California bay (*Umbellularia californica*), Pacific madrone (*Arbutus menziesii*) and red alder (*Alnus rubra*).

Due to an extensive logging history, forests on STC lands were predominately even-aged young stands between 30–60 yr of age. Approximately 1.0% of the area was old growth forest (>200-yr old), all of which occurred as isolated stands <40 ha in size. Variability in terrain, past harvest practices, reforestation practices and species composition influenced the structure of stands. These stands varied from young forest with little variation in tree size to areas having residual old trees scattered within young forest. Residual trees were larger remnant trees from the original forest stand. These residual trees increased variation in tree sizes and stand structure, but the density of these trees across the landscape was low.

METHODS

We measured landscape characteristics around 60 Northern Spotted Owl nest sites located during 1990 and 1991. Nests were located from March–June following Forsman (1983). All nest sites included in this study were from different owl pairs. We defined the landscape as the mosaic of forest-cover types surrounding an owl nest within a 0.8 km-radius circle (203 ha) centered on the nest site. This plot size allowed minimal or no overlap among plots for pairs that nested in close proximity. In many cases, a larger circle would have encompassed the nest or roost area of other pairs of Northern Spotted Owls. This reduced the chance of assigning habitat characteristics to an owl site that may not have been available to those owls due to territoriality among sites.

We plotted nest locations on 1988 color aerial photographs and planimetric maps each having scales of 1:12 000. To reduce errors in area measurement from

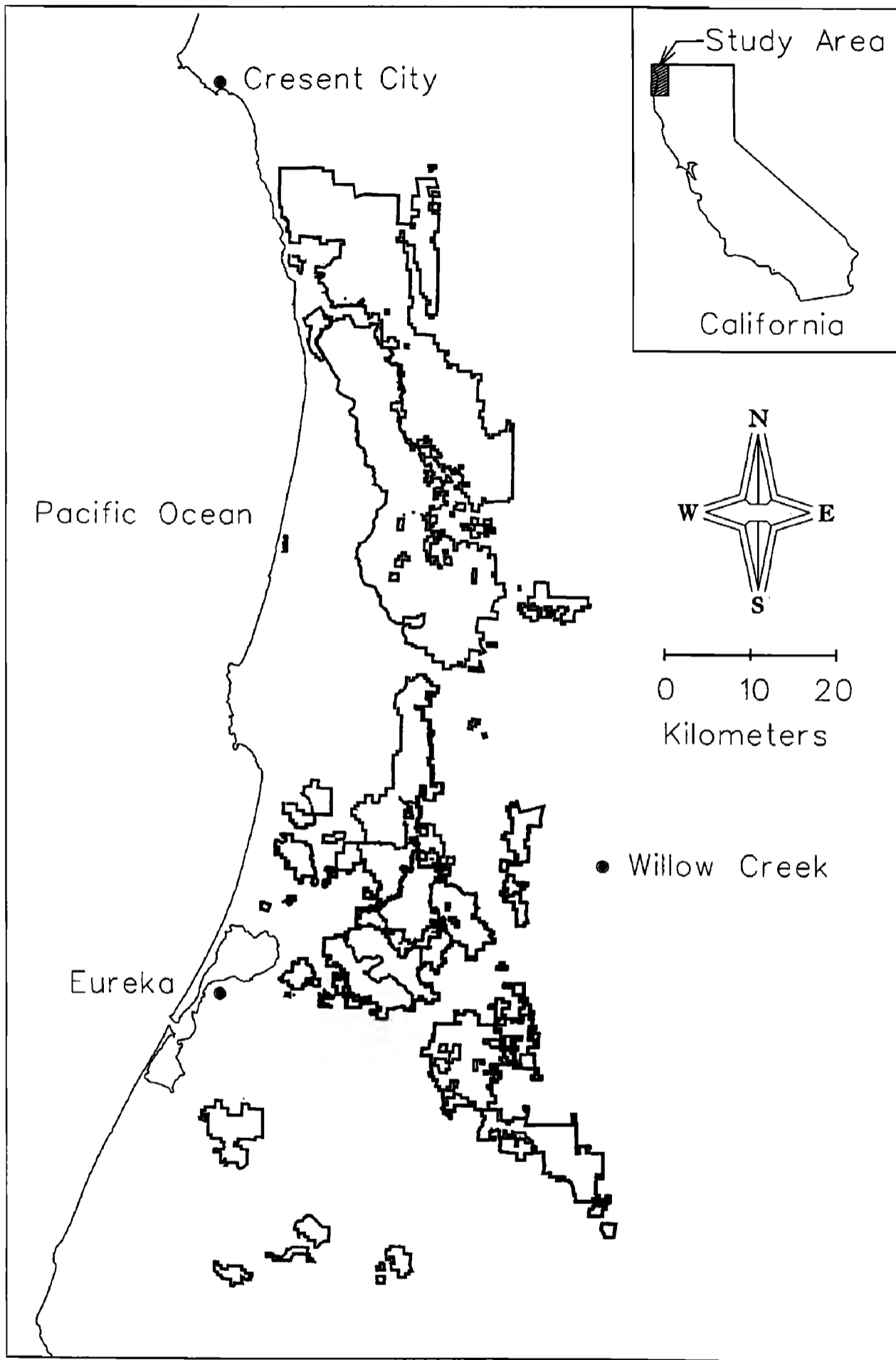


Figure 1. Location of Northern Spotted Owl nest-site study area in the coastal redwood zone of northwestern California, 1990–91.

slight deviations in scale on aerial photos, all sites were plotted on the planimetric maps with the plot boundary drawn around them (Avery and Berlin 1985:82). Maps were generated from a geographical information system (GIS) and overlaid with forest cover-type boundaries. STC maintains a current database of forest types and stand ages based on periodic timber inventories and harvest dates. The combination of large-scale color air photos and the GIS database increased the efficacy of our mapping technique. All forest information was updated to reflect recent timber harvesting.

Within each landscape plot, we estimated the age classes and species composition of all stands present. The dominant overstory vegetation was classified into five cover-types: redwood, redwood/Douglas-fir, Douglas-fir, hardwood and nonforest. Conifer cover types often included a minor component of hardwood species. We initially classified seven stand age classes: 0–7, 8–30, 31–45, 46–60, 61–80, 81–200 and >200 yr of age. However, we collapsed the latter three classes into a single class of >60 yr of age because older stands were scarce as well as uneven in age and spatial distribution. Although the designation of age classes was subjective, they were determined from a biological and a forest management perspective as follows. The 0–7 yr class represented the period during which recently clearcut areas reestablished a dense cover of shrubs and seedlings and evidence (i.e., stick houses) of dusky-footed woodrats (*Neotoma fuscipes*), the owls' primary prey, began to appear on the sites. The 8–30 yr class included a wider range of stand conditions but, in general, it supported woodrat populations (Sakai and Noon 1993, Hamm 1995). In addition, older stands in this age class were potentially reaching a stage of development suitable for owl foraging (Forsman et al. 1984). The 31–45 yr class was chosen to include a seral stage at which stands began to develop structural characteristics associated with owl use in other parts of their range. In general, this age class was suitable for roosting and foraging but, in some instances, it was suitable for owl nesting (Folliard 1993). The 46–60 yr age class was important to evaluate because most stands in this class were reaching an age and size permitting timber harvest, and they were generally suitable as nesting habitat for owls. The >60 age class was important to evaluate because shorter harvest cycles will often preclude the development of this age class in future managed landscapes.

We mapped each landscape plot as polygons corresponding to these cover types and age classes. After mapping all the polygons in the circular plot, we calculated the area of each polygon using a dot grid (Avery and Berlin 1985:85–86). Because a combination of aerial photographs and GIS were used for polygon mapping, we did not have a complete GIS database to use for area calculations and other measurements. We estimated the amount of total edge, both low-contrast and high-contrast, within the landscape plot by measuring the perimeter of all polygon boundaries with a map wheel. We defined low-contrast edge as the juxtaposition of two distinct cover types or different age classes of the same cover type. We defined high-contrast edge as the boundary between stands ≥ 31 -yr old and nonforest or stands 0–7-yr old. We considered low-contrast edge a measure

of forest heterogeneity and high-contrast edge a measure of forest fragmentation. We recognize that low-contrast edge was the result of past timber harvest and was also a form of forest fragmentation. Total length of roads in the plot and the distance from a nest site to the nearest water source were also measured with a map wheel. We calculated slope position of the nest site as the ratio between the distance from the nest site to the bottom of the slope and the total distance from the bottom of the slope to the ridgetop. To avoid bias in measurements, distances were measured along a line that passed through the nest site that was perpendicular to the ridgetop and bottom of the slope. Slope position varied from zero to one with zero being the bottom of the slope and one being the ridgetop.

To test the null hypothesis that no differences in landscape variables existed between nest and random sites, we selected a point at a random direction and distance (≤ 19.2 km, based on the maximum spacing of habitat conservation areas for Northern Spotted Owls; see Thomas et al. 1990) from each nest site. Random points were rejected if they fell beyond STC ownership and could be no closer to a known owl site than the minimum distance observed between two nesting pairs (670 m) in our study area. Data from random plots were collected following the same procedure used at nest sites.

Northern Spotted Owl pairs were considered reproductively successful if they fledged at least one owlet. To determine reproductive success of nesting Northern Spotted Owls, daytime visits were conducted at nest sites to search for fledged owlets. Minimum estimates of fledging success were calculated by summing the total number of owlets fledged by all pairs and dividing by the number of pairs. It was possible that we did not find all fledged young at nest sites, and thus our estimates of productivity were minimum estimates.

STATISTICAL ANALYSES

We calculated correlations among all the variables to reduce the dataset. Variables were considered correlated if the correlation coefficient was ≥ 0.80 . If variables were correlated, the one that seemed most biologically relevant was retained for further analysis.

We assessed all variables for normality within groups (i.e., nest and random landscape variables) using the Wilk-Shapiro test (Shapiro and Francia 1972). Variables that exhibited nonnormality were subjected to a square-root transformation to increase normality and homogeneity among variances (Zar 1984:241). Following transformation, most variables were normal or near normal in distribution.

To test for group differences between nest and random landscapes, we used multivariate analysis of variance (MANOVA) (Wilkinson 1990) with site status (nest or random) as the independent variable. Although some of the dependent variables were not normally distributed, the MANOVA procedure (two-group case) is robust to deviation from this assumption (Seber 1984:113). A test for homogeneity of the covariance matrices (Morrison 1976:252) indicated that the null hypothesis of equality could not be rejected at the 5% level ($\chi^2 = 21.5$, $df = 15$, $P = 0.121$).

Following the MANOVA, univariate tests were per-

Table 1. Summary statistics for landscape variables measured within 203-ha circular plots centered on 60 Northern Spotted Owl nest sites and 60 random sites from northwestern California, 1990 and 1991.

VARIABLE	NEST LANDSCAPES MEAN \pm SD	RANDOM LANDSCAPES MEAN \pm SD	F	P
0–7-yr-old forest, ha	17.2 \pm 25.8	23.3 \pm 38.6	0.065	0.800
8–30-yr-old forest, ha	23.9 \pm 38.0	53.1 \pm 68.6	4.376	0.039
31–45-yr-old forest, ha	45.6 \pm 60.1	29.3 \pm 49.5	4.341	0.039
46–60-yr-old forest, ha	55.4 \pm 63.7	33.9 \pm 56.4	5.314	0.023
>60-yr-old forest, ha	41.5 \pm 45.7	40.7 \pm 48.8	0.122	0.728
Nonforest area, ha	19.7 \pm 19.2	21.9 \pm 33.6	0.630	0.429
Total edge, km	8.1 \pm 3.1	6.4 \pm 2.9	9.273	0.003
High-contrast edge, km	4.2 \pm 2.9	4.0 \pm 3.2	0.172	0.679
Position on the slope	0.35 \pm 0.23	0.52 \pm 0.28	14.034	<0.001
Distance to water, m	136.7 \pm 96.7	190.9 \pm 141.0	4.711	0.032
Length of roads, km	3.7 \pm 2.1	4.8 \pm 2.7	5.067	0.026

formed for each dependent variable to determine which variables contributed to group differences. Dependent variables that differed ($P < 0.05$) between nest and random sites were entered into a stepwise discriminant analysis (Hintze 1997). We used a stepwise variable selection procedure with variables having a probability to enter the model of $\alpha = 0.15$ and a probability $\alpha = 0.05$ for removal from the model. Cohen's kappa (Titus et al. 1984) was used to determine if the model classified groups significantly better than chance. A *t*-test was used to test for differences in landscape variables between reproductively successful and unsuccessful pairs.

RESULTS

Landscape features differed between Northern Spotted Owl nest sites and random sites (Wilks' $F = 6.073$, $P < 0.001$). Subsequent univariate tests showed differences between eight of the 12 dependent variables included in the MANOVA (Table 1). Random landscapes had more 8–30-yr old forest, while there was more forest in the 31–45 and 46–60 yr age classes in nest landscapes. The amount of older forest age class (>60-yr old) was not different between the groups. The amount of 0–7 yr age class, created by recent clearcut logging, was also not different.

The >60-yr old forest age class was composed of three age classes, 61–80, 81–200 and >200 yr. We did not believe that grouping these classes biased the results, because the group means for these classes were similar. The mean area of forest at nest and random sites, respectively, were 24.3 and 28.2 ha in the 61–80 yr class, 12.1 and 11.4 ha in the 81–200 yr class and 5.2 and 1.1 ha in the >200 yr class. Nest sites were lower on the slope ($P = 0.001$) and closer to water ($P = 0.032$) than random sites (Table 1). The total length of roads was

lower ($P = 0.026$) within nest landscapes. The amount of total edge in nest landscapes was higher ($P = 0.003$) than in random landscapes (Table 1). Total edge represents a combination of fragmentation and heterogeneity of the forested landscape. When considering just high-contrast edge, there was no difference ($P = 0.679$) between groups. This result was consistent with the lack of difference in the amount of 0–7 yr age class.

Variables significantly different between nest and random sites were entered into a stepwise discriminant analysis. Four variables were selected for the discriminant function model (Table 2). The model had an overall correct classification rate of 72.5%, which was better than chance alone (Cohen's kappa = 0.45, $P < 0.001$). Nest landscapes were correctly classified 71.7% of the time, whereas 73.3% of random landscapes were correctly classified.

Of the 60 Northern Spotted Owl pairs studied, 47 pairs successfully fledged at least one owlet, eight pairs were unsuccessful and the reproductive status of two pairs was undetermined. Three pairs that were unsuccessful in 1990 successfully fledged young in 1991, but were excluded from this analysis due to shifts in nest locations that would have required additional mapping of newly centered nest plots. Habitat variables that were significant in the discriminant analysis were tested for differences between reproductively successful ($N = 47$) and unsuccessful pairs ($N = 8$), and no differences were found (Table 3). However, the small sample size of reproductively unsuccessful pairs probably limited our ability to detect differences.

Table 2. Summary of stepwise discriminant analysis for comparison of 60 Northern Spotted Owl nest landscapes with 60 random landscapes in northwestern California, 1990 and 1991.

VARIABLE	STEP ENTERED	WILKS' LAMDA	P	COEFFICIENT ^a
Position on slope	1	0.894	<0.001	0.648
Total edge, km	2	0.812	<0.001	-0.739
31-45-yr-old forest, ha	3	0.719	0.027	-0.575
46-60-yr-old forest, ha	4	0.688	0.025	-0.501

^a Standardized canonical coefficients.

DISCUSSION

We found significant differences in landscape features between Northern Spotted Owl nest and random landscapes, which suggested that owls selected nest areas based on habitat characteristics at scales larger than the forest stand. Other studies have evaluated Northern Spotted Owl habitat on a landscape level by focusing on the amount of mature and old-growth forest across the landscape (Ripple et al. 1991, Lehmkuhl and Raphael 1993, Meyer et al. 1998). Throughout most of its range, old-growth forest was an important indicator of site occupancy by Northern Spotted Owls (Forsman et al. 1977, Forsman et al. 1984), and increased amounts of older forest may contribute to increased reproductive success (Bart and Forsman 1992). Carey et al. (1990) found that Northern Spotted Owl home ranges contained more old growth than in the surrounding landscape, and there was a negative correlation between home range size and the proportion of old growth in the home range. Greater amounts of older forest types across the landscape presumably constitutes better habitat for Northern Spotted Owls, and management recommendations have been suggested based on this criteria (Ripple et al. 1991, 1997).

Our study investigated correlative relationships between owl nest-site locations and specific char-

acteristics of the surrounding forest environment. Although we did not demonstrate cause and effect relationships, description of the observed associations provide a greater understanding of Northern Spotted Owl biology in this restricted portion of the range. Another limitation was the use of circular plots to characterize owl habitat when actual home range configurations may exhibit different habitat patterns (Lehmkuhl and Raphael 1993). Furthermore, circular plots may include unused areas. Information on owl home range size and configuration is lacking for the redwood zone. However, we believe that all habitat in the 203-ha plots was likely to be used by owls because this size was not overly large compared to home ranges reported in California (Solis and Gutiérrez 1990, Zabel et al. 1995), and because circles were centered around nest sites.

In our study area, forest age classes of 31-45 and 46-60 yr were the most prevalent age classes in landscapes of nesting Northern Spotted Owls. We believe these mid-aged forest stands represented habitat used for nesting, roosting and foraging whereas stands <30 yr of age were generally lacking characteristics of owl nesting habitat. The majority (53%) of nests were located in stands 35-60-yr old, while 30% were in stands 61-80-yr old and 17% in stands >80-yr old. No nests were found in

Table 3. Univariate test statistics for landscape variables at nest landscapes compared between successful and unsuccessful Northern Spotted Owl pairs from northwestern California, 1990 and 1991.

VARIABLE	SUCCESSFUL	UNSUCCESSFUL	<i>t</i>	<i>P</i>
	(<i>N</i> = 47) MEAN ± SD	(<i>N</i> = 8) MEAN ± SD		
Total edge, km	8.0 ± 3.2	8.2 ± 2.9	0.25	0.805
31-45-yr-old forest, ha	44.5 ± 59.9	46.4 ± 62.7	0.06	0.950
46-60-yr-old forest, ha	62.6 ± 65.2	44.9 ± 61.9	1.02	0.314
Position on slope	0.33 ± 0.22	0.43 ± 0.33	1.02	0.312

stands <35-yr old. Many of the stands in these age classes used by owls contained a component of residual trees that added increased structure and complexity to the stands (Folliard 1993). Concentrations of residual trees around nest areas may also contribute to higher reproductive success of owls on managed landscapes (Thome et al. 1999). Bias and Gutiérrez (1992) found California Spotted Owl (*S. o. occidentalis*) roost and nest sites in pole-medium successional stage habitats with residual old-growth trees present in the stands. They suggested that forest structure, not forest or tree ages *per se*, was important to California Spotted Owls. Although the amount of forest older than 60 yr was not different between groups at the landscape level, these areas were used for nesting at the stand level (Folliard 1993). Because stands >60-yr old occurred at a low frequency across the landscape and were scattered in distribution, there was little opportunity for owls to nest in and use a landscape that encompassed a large proportion of this age class.

Carey et al. (1990) found that the amount of old growth in Northern Spotted Owl home ranges was less variable than home range size itself. This implies that owls are maintaining home ranges of sufficient size to encompass some minimum amount of suitable habitat required for their life needs. The threshold of required habitat will likely vary depending on the spatial distribution of remaining forest and the availability of prey species. We found owls using small patches of older forest (>60-yr old) if the surrounding landscape had a high proportion of forested area >30-yr old. Small patches of older forest provided roosting and nesting areas, while the surrounding younger forest presumably provided foraging habitat. Young landscapes that lacked patches of older forest (>60-yr old) or residual trees did not support nesting owls.

The amount of total edge was an important variable distinguishing nest from random sites. Nest areas had more low-contrast edge, indicating that habitat pattern surrounding nest sites had more spatial heterogeneity due to a diverse matrix of differing age classes and cover types. Our index of forest fragmentation (amount of high-contrast edge) and amount of recent clearcut area (0–7 yr age class) showed no difference between nest and random sites. Our findings were consistent with those of Meyer et al. (1998) who also found that the amount of clearcut area did not differ between owl and random sites within a 0.8-km radius circle.

The increased spatial or forest heterogeneity (i.e., greater amounts of low-contrast edge) in nest areas may contribute to a higher abundance and diversity of prey species for owls on the study area. The abundance and diversity of available prey species may influence habitat use patterns of Northern Spotted Owls (Carey et al. 1992). Studies in northwestern California indicate that woodrats are abundant in young seral stages (Raphael 1988, Sakai and Noon 1993, Hamm 1995). Hamm (1995) studied woodrats on our study area and found the highest densities in young stands 5–20-yr old. Most of these young stands where woodrats are abundant create low-contrast edge when adjacent to older forest age classes. Based on pellet analysis, woodrats represented a significant component of the owls' diet on our study area (Diller unpubl. data). Although owls may not have foraged directly in such areas, they probably foraged near edges where older forest adjoins younger patches of prey habitat. In northwestern California, Northern Spotted Owl foraging locations have been found closer to edges where woodrats represent the major prey species (Zabel et al. 1995).

In addition to edge providing foraging opportunities, young forest patches likely provide a "reservoir" of prey that disperse into adjacent stands used by Northern Spotted Owls (Sakai and Noon 1993). Boxall and Lein (1982) found that Snowy Owls (*Nyctea scandiaca*) selected territories with higher amounts of edge habitat (fencerows and roadside ditches) that had a high abundance of prey. Although prey was abundant in edge habitats, they were usually not available to Snowy Owls until they moved into adjacent fields.

The high amounts of total edge were at least partly related to the history of timber harvest in the area. Because most of the study area occurred in young and mid-aged forests, the owl sites were the result of past and ongoing timber harvests. Our results support the hypothesis that, in northern California, a certain degree of openness created by timber harvest may be beneficial to Northern Spotted Owls by providing younger seral habitat for major prey species such as woodrats (Sakai and Noon 1993). On our study area, Hamm (1995) found that woodrat abundance declined sharply in stands >30-yr old. However, Northern Spotted Owls may avoid areas that become overly fragmented by timber harvest to reduce exposure to predators (Gutiérrez 1985) or to lower interactions with potential

competitors such as Barred Owls (*Strix varia*) (Dark et al. 1998).

Northern Spotted Owl nest sites were most commonly located on the lower portions of slopes and rarely near ridge tops. The tendency to locate nests on the lower portions of slopes has been documented previously (Forsman et al. 1984, LaHaye 1988, Blakesley et al. 1992, Hershey et al. 1998). Northern Goshawks (*Accipiter gentilis*), another forest raptor, have also been observed nesting lower on slopes (Hayward and Escano 1989). Lower portions of slopes may provide more favorable conditions for the development of large trees that provide nest sites for owls (LaHaye 1988). However, this hypothesis does not adequately explain the phenomenon on our study area because even though Northern Spotted Owls nested lower on slopes, many nests were in relatively young trees. Most of the old growth forest has been previously harvested on our study area and across the landscape there is no concentration of large trees lower on slopes. Although statistically different, the magnitude of difference in slope position between nest and random sites (0.35 vs. 0.52, respectively) may not be biologically significant; both could be viewed as midslope.

The predictive capability of the discriminant model had a correct classification rate of 72.5%, which was significantly greater than chance. Misclassification of sites, however, indicates that some nest and random areas had similar habitat characteristics. Explanations for the similarity of some nest and random sites are: (1) random sites may have been suitable as nest areas, but were not yet colonized by owls; (2) territoriality among owls could preclude areas from additional occupancy; and (3) quantification of owl sites based on vegetative parameters alone may not represent the full suite of factors that influence site selection at a larger scale. Some measure of prey abundance in different habitats may reveal further differences between nest and random areas. The associated prey base and its availability can be important determinants of suitable owl habitat (Carey et al. 1992). In some areas, the density of raptors is largely determined by prey abundance, with the availability of suitable nest sites having little influence on breeding densities (Korpimäki and Norrdahl 1991). The influence of prey abundance and availability on Northern Spotted Owl occurrence in managed forests deserves further investigation.

Our study occurred within the coastal Redwood

Vegetation Zone, considered to be a unique portion of the Northern Spotted Owl range (Thomas et al. 1990). The coastal forests of redwood and Douglas-fir in northwest California have unique characteristics that contribute to the rapid development of Northern Spotted Owl habitat on managed landscapes. These characteristics include coppice growth (i.e., vegetative reproduction) of redwoods and several species of hardwoods and favorable growing conditions that result in rapid growth of all vegetation. In addition, the mild coastal climate may reduce thermoregulatory demands on owls in young forests (Ting 1998).

In spite of great differences in habitat types, age class distributions and management histories, Northern Spotted Owl nest-site selection in the redwood zone showed similarities with habitat selection in other portions of its range. Although our study area lacked significant amounts of old-growth forest, Northern Spotted Owls selected nest landscapes with greater amounts of the oldest forest age classes available. This was consistent with other studies in Oregon and Washington (Ripple et al. 1991, Lehmkuhl and Raphael 1993, Meyer et al. 1998) and California (Hunter et al. 1995, Gutiérrez et al. 1998). Because our study area was primarily young and mid-aged forest stands, our results suggested that forest age is probably less important than aspects of forest structure when identifying suitable habitat for Northern Spotted Owls. In addition to greater amounts of older forest age class (46–60 yr), the proportion of this age class in nest landscapes was similar among other studies. The mean area of forest stands ≥ 46 -yr old in our study was 97 ha, which was 48% of the 203-ha circle. Hunter et al. (1995) reported a similar mean of 94 ha of mature and old-growth forest in 200-ha circular plots centered on Northern Spotted Owl nest sites. Lehmkuhl and Raphael (1993) found that Northern Spotted Owl home ranges on the Olympic Peninsula in Washington contained an average of 44% owl habitat (old-forest stands or 80–100-yr old stands with an overstory of remnant old trees). Northern Spotted Owl home ranges in southern Oregon contained from 27–75% old growth (Carey et al. 1990). Although the spatial scales varied among these studies, the similar proportions in suitable habitat may indicate a potential threshold of suitable habitat to support owl occupancy. Landscape features such as amount of older forest and the proportion of older forest

around owl sites are likely to be factors that influence site selection on managed forestlands.

The impacts of timber harvest on Northern Spotted Owl occupancy at the landscape or watershed level depend on the extent and rate of harvest in the area. Initially, when large amounts of mature forest are present, negative impacts from dispersed clearcutting are likely to be minimal. However, if harvest continues and larger areas become dominated by young forests, the suitability of the landscape as nesting habitat for Northern Spotted Owls will diminish. Landscapes extensively harvested over the last 30 yr were the least used for nesting by Northern Spotted Owls in our study. Furthermore, prolonged timber harvest within Northern Spotted Owl territories may negatively influence reproductive success prior to affecting site occupancy (Thome et al. 1999).

Our data suggested that, to maintain Northern Spotted Owls in managed forests of the redwood zone, $\geq 50\%$ of the landscape or area surrounding nests should be in forests > 45 -yr old. In addition, clearcut harvesting on a landscape level scale should be distributed over time and space to produce a mix of age classes that provide for Northern Spotted Owls and early seral prey species such as woodrats. Staggering harvest would reduce the occurrence of large areas that are unsuitable for nesting. Clearcut harvesting should also retain green trees, particularly those with decadence or structural deformities, to provide older forest structure in regenerating stands.

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